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Depth and water temperature drive elevated post-release mortality of gray triggerfish (*Balistes capriscus*)

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Post-release mortality of regulatory discards is a persistent challenge in marine fisheries management, with inaccurate estimates risking biased stock assessments and ineffective regulations. We used data from a multi-year, large-scale mark–recapture program to estimate post-release mortality of gray triggerfish (*Balistes capriscus*), a highly targeted reef-associated fish in Florida's coastal and offshore waters. We developed a discrete-time relative-risk model that posited post-release survival as a nonlinear function of depth and sea surface temperature (SST), while accounting for spatiotemporal variation in fishing effort and uncertain reporting rates. Our best-fitting model suggested post-release mortality increases with both depth and SST, enabling temporally explicit, observation-based predictions. Our estimates of post-release mortality are consistent with recent studies reporting high post-release mortality for this species. Moreover, our results align with recent evidence that post-release mortality has been increasing over time as anglers fish in deeper waters farther offshore. The strong temperature effect is also consistent with recent findings of heightened thermal sensitivity in gray triggerfish compared to other highly targeted reef fishes. Together, these results highlight key environmental drivers of post-release mortality and provide an approach for improving stock assessments and management strategies for this and other ecologically and economically important fishery species.

KEYWORDS

fisheries management, mark-recapture, post-release survival, recreational fisheries, reef fish

1 Introduction

Mortality of released fish continues to pose a major obstacle for effective fisheries management. Regulatory discards arise when fish must be released to comply with harvest restrictions, including limits on size, season, area, or daily harvest (i.e., bag limits; Bellido et al., 2011; Tetzlaff et al., 2013). Although such regulations are intended to reduce overall removals from exploited stocks, the survival of released individuals is often uncertain (Benoît et al., 2012). If post-release mortality is not estimated accurately, evaluations of fishing pressure and stock condition can be biased, weakening the basis for management decisions (Punt et al., 2006; Cook, 2019). Consequently, accurate, species-specific quantification of post-release mortality is essential for sustainable management, particularly for intensely managed species where discards can far exceed landings.

Post-release mortality is influenced by environmental conditions as well as species-specific morphology and physiology. Benthically-oriented fish captured from depth are especially prone to barotrauma, where rapid gas expansion during ascent damages tissues and internal organs (Ferter et al., 2015; Rankin et al., 2017; Runde et al., 2019). Warm water generally increases metabolic rates and oxygen demand, which, in turn, exacerbates capture-related stress and post-release mortality risk (Giomi et al., 2008; Kraak et al., 2019; Schram et al., 2023; Rubalcaba et al., 2020; Davis, 2002). Species-specific physiology and morphology can further exacerbate these effects: large swim bladders relative to body size increase the likelihood of internal injury during ascent and difficulty re-submerging (e.g., Burns, 2009), while laterally compressed fish with narrow body cavities may be especially prone to organ displacement and tissue damage (Colotelo et al., 2012; Runde et al., 2019). Limited cardiovascular or aerobic scope can also reduce thermal tolerance, allowing warmer waters to interact with other stressors to heighten mortality. These factors underscore the importance of incorporating context- and species-specific post-release mortality estimates into stock assessments to support effective management and conservation of exploited fish populations.

In this study, we used data from a long-term, large-scale mark–recapture program to estimate relative post-release mortality for gray triggerfish (*Balistes capriscus*), a highly targeted reef-associated species in the Gulf of America (Gulf). Gray triggerfish have been subject to intensive management due to high exploitation and ongoing concerns regarding stock status (SEDAR43, 2015). While earlier estimates suggested relatively low (~5%) post-release mortality, more recent work using advanced mark–recapture and acoustic telemetry methods suggests substantially higher rates (i.e., 26 - 66%; Runde et al., 2019; Bohaboy et al., 2020), with important implications for stock assessments and management. Analyses of gray triggerfish post-release condition, based on external barotrauma and swim score — both indicators of mortality — suggest that gray triggerfish are more thermally sensitive than other reef-associated species (Hyman et al., 2026), underscoring the potential impact of ocean warming on post-release survival.

We developed a discrete-time survival model to estimate relative post-release mortality using conventional tagging data collected from 2022 to 2024, with relative recapture rates serving as a proxy for relative survival. We then modeled post-release mortality as a function of depth and sea surface temperature (SST)—our primary predictors of interest—and incorporated observational data from the for-hire recreational fishery to generate temporally explicit predictions of post-release mortality along the west coast of Florida. Our results provide new insights into emerging environmental drivers of post-release mortality in gray triggerfish, thereby supporting improved stock assessment and strategies for more effective management of this ecologically and economically important species.

2 Methods

2.1 Data sources

We analyzed tag-return records for gray triggerfish collected from 2022 through 2024 as part of the Florida Fish and Wildlife Conservation Commission (FWC), Fish and Wildlife Research Institute's (FWRI) For-Hire At-Sea Observer Survey (hereafter, the Observer Program). The Observer Program, initiated in 2009, represents a partnership between FWRI biologists and the for-hire recreational fishing sector in Florida. As part of this program, trained observers accompany recreational anglers on randomly selected for-hire (i.e., charter and head boat) trips each month based on a stratified sampling design. Currently, approximately 20% of federally permitted for-hire operators in Florida's Gulf waters participate. The Florida Panhandle is a focal area for this stock, with landings in Florida representing 72% of total recreational landings in the Gulf. Consequently, most (92%) of gray triggerfish landings reported by the program occur offshore along the Florida Panhandle. Importantly, limiting analysis to a relatively narrow geographic range reduces the likelihood of spatially variable reporting rates, which could bias inference. We therefore restricted our analyses to data collected from this region.

During observed trips, FWRI scientists record information on recreational hook-and-line activities at each fishing "station." A station is defined as a unique 1-minute grid cell of latitude and longitude, with new stations logged whenever a vessel crosses into another grid cell. Observers record geographic coordinates, depth, and time for each station.

Tagging of priority reef fish species is conducted by FWRI to evaluate post-release mortality and movement. Discarded fish are fitted with Hallprint dart tags, inserted laterally near the first dorsal fin and secured between the pterygiophores on the left side of the body (Sauls, 2014). Tags consist of a monofilament streamer imprinted with a unique identification number, a toll-free reporting hotline, an email contact, and the word "reward." The program is publicized statewide, and anglers returning tags receive a free t-shirt and a summary of information about their fish (e.g., time-at-large, growth, and movement history) to incentivize participation (Sauls, 2014).

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2.1.1 Predictors of post-release mortality

We considered a suite of covariates expected to influence post-release mortality, with particular emphasis on capture depth and SST. Fishing station depth, used as a proxy for the depth of capture, was determined using an onboard depth sounder at each fishing station. Although fishing station depth should always be deeper than the true depth of capture, we assumed that these quantities were proportional (i.e., deeper fishing station depths corresponded with deeper depths of capture). To account for thermal effects, we used SST as a proxy for thermal stress, extracting temperature data from the HYbrid Coordinate Ocean Model (HYCOM), a high-resolution ocean circulation model developed by scientists at NOAA and the Naval Research Laboratory, along with a number of academic collaborators (Halliwell, 2004; Chassignet et al., 2007). Validation studies have demonstrated close agreement between HYCOM reanalysis temperature estimates and *in situ* observations (Thorr et al., 2025), supporting its application in fisheries research. Specifically, we employed the HYCOM-TSIS GOMb0.01 product, which provides hourly Gulf metrics since 2001 at ~1 km^2 spatial resolution (HYCOM, 2020). To match HYCOM SST data with observer records, each release event was assigned a unique spatiotemporal index consisting of date, latitude, longitude, and hour of release. HYCOM SST values were extracted using a nearest-neighbor approach, whereby each observation was assigned the temperature from the geographically nearest HYCOM grid cell (usually an exact match). Because HYCOM SST is provided at discrete temporal intervals, temporal mismatches were resolved by assigning the SST value from the time step closest to the recorded release hour. No spatial interpolation was performed.

Additional covariates were also considered but ultimately excluded from the final model framework. Descending device use was not considered due to an insignificant number of tagged gray triggerfish from the observer dataset being descended. Moreover, seasonal categorical variables were confounded with SST; therefore, we made the decision to retain SST – the predictor thought to be the primary driver of post-release outcomes. Due to their unique anatomy, deep-hook injuries are extremely rare in gray triggerfish and were therefore excluded as a covariate (Runde et al., 2019). Instead, the seven tagged fish with deep-hook trauma were simply removed from our dataset prior to analysis. Fish size has been shown to influence post-release mortality, as larger individuals typically fight longer and experience greater physiological stress during capture (Martin et al., 2023; Zimmermann et al., 2025). However, the vast majority of discarded fish (~75%) fell between 250 and 350 mm, and nearly all (95%) were between 250 and 400 mm. The lower bound of these sizes is likely constrained by catchability due to the large circle hooks used by recreational anglers in the northern Gulf and the relatively small mouth gape of the species (Garner et al., 2017). The upper bound for released fish is limited by the fact that fish over the minimum size threshold (~380 mm) are frequently harvested (as opposed to being released). Given this lack of sufficient contrast, size was not included as a predictor. Finally, although other environmental or capture-released covariates (e.g., dissolved oxygen, handling time, etc) could presumably affect post-release mortality, these variables were not available for inclusion in our analyses.

2.2 Analysis

The model follows a modified Cormack-Jolly-Seber (CJS) framework by partitioning the discrete-time probability of observing a recapture at time t into multiple sequential survival and re-encounter probabilities. It follows a similar sequential structure to the release–recapture model of Shertzer et al. (2018); however, our formulation marginalizes over the latent state process (i.e., whether a fish remains at risk of recapture at a given time step) rather than modeling these intermediate states explicitly. Here, we modified the CJS likelihood to encompass: (1) the probability of surviving the immediate post-release period, denoted ψ; (2) the probability of remaining at risk at each time step from release to time t, conditional on surviving post-release, denoted ϕ_t; (3) the probability of being re-encountered by an angler at each time step from release to t, denoted η_t; and (4) the probability that a re-encountered fish is reported, ξ, which is assumed to be constant over time (Figure 1, Cormack, 1964; Jolly, 1965; Seber, 1965; Schofield, 2007).

For a tagged fish to be observed as recaptured, it must survive release, remain at risk until time t, be re-encountered, and be reported. We selected a three-month (quarterly) interval to balance temporal resolution with sufficient numbers (i.e., n ≥ 20) of tagged fish at risk within each interval, resulting in T = 13 temporal intervals between January 2022 and December 2024 (our censoring date). In general, for any $t \geq t_0$, the probability of recapture for fish i is:

$$Pr(R_i = t) = \psi_i \prod_{s=t_0}^{t-1} (\phi(1 - \eta_{i,s}))\phi\eta_{i,t}\xi$$

Meanwhile, the probability of never being recaptured (censoring) is the complement of the summed recapture probabilities:

$$\begin{aligned} Pr(R_i = 0) &= 1 - \sum_{t=t_0}^{T} Pr(R = t) \\ &= 1 - \sum_{t=t_0}^{T} \left[\psi_i \prod_{s=t_0}^{t-1} \Big(\phi(1 - \eta_{i,s}) \Big) \phi\eta_{i,t}\xi \right] \end{aligned}$$

This model framework makes several simplifying assumptions to remain tractable given limited information. First, we assume that the reporting ξ is constant across fishing modes and, crucially, is not dependent on covariates thought to impact survival (e.g., anglers fishing in deeper water report recaptured fish at rates comparable to those in shallow water). While we have no evidence, nor any *a priori* reason to suggest reporting rates would vary with covariates of interest, should such correlations exist, they would result in informative censoring and necessarily bias inference. Second, we assume that mortality incurred through the tagging process itself is negligible. Finally, our strongest assumption is that once a fish is re-encountered by an angler, it is effectively removed from the at-risk population. Removals occur either because re-encountered fish are reported as recaptures or, if not reported, are considered permanently lost to the observed population (e.g., harvested or

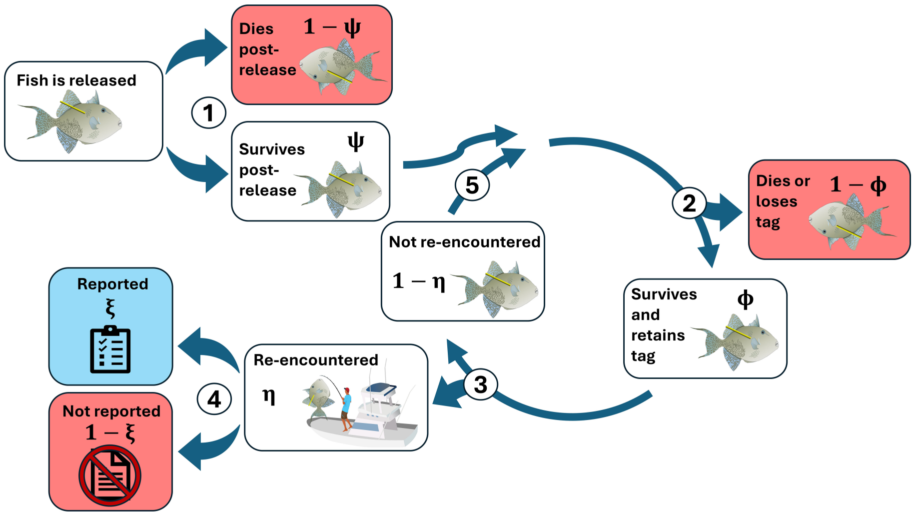

FIGURE 1
Conceptual diagram of processes determining the fate of a tagged gray triggerfish at each time step, resulting in either recapture at time t (R=t, blue box) or loss (R = 0, red boxes). The sequence of events is: (1) survival during the immediate post-release period with probability ψ, dependent on injuries sustained during capture; (2) remain in the risk pool with probability ϕ dependent on natural mortality/tag shedding; (3) re-encountered with probability η depending on recreational angler effort, (4) if re-encountered, reported with constant probability ξ or (5) if not re-encountered, fish that remain at risk at the end of a time step repeat steps 2–5 until re-encountered, lost, or censored at the end of the study. Graphics were obtained, in part, through the Integrated Application Network (IAN) Image Library.

released without a tag). This assumption, while unrealistic (i.e., it is likely that at least some re-encountered but unreported fish are thrown back with intact tags), is necessary to avoid estimating an unknown number of re-releases and associated post-release survival probabilities given unknown future conditions. If this assumption is violated, post-release survival estimates may be underestimated depending on factors such as the true reporting rate, re-release rate, and degree to which survival from sequential releases is correlated. We elaborate further on this limitation and its potential consequences in detail in the discussion.

Post-release survival, ψ, represents the probability that a fish survives the immediate post-release period. We modeled ψ as a function of multiple environmental and fishing–related predictors, allowing each predictor to enter through its own transformation:

$$\psi_i = \exp\left(\beta_0 + \sum_{k=1}^{K} \beta_k f_k(x_{i,k}|\theta_k)\right)$$

where $x_{i,k}$ is the k^{th} covariate (e.g., depth, SST) for fish i, $f_k(\cdot)$ is a chosen threshold function with a parameter vector θ_k, and β_k is the corresponding effect size. Here, β_0 denotes a log baseline post-release survival rate, which is scaled by environmental covariates. All β_k coefficients are estimated in log space and then constrained to be negative. Alternative model structures considered are detailed in the Model specification section below.

The probability that a fish remains alive with an intact tag at time t (ϕ) depends on natural mortality and tag shedding, which are assumed to be invariant across time and space. We modeled the probability of loss within the interval t as:

$$\lambda = 1 - \exp(-\exp(\gamma))$$

where γ represents the baseline log-hazard of natural mortality and tag shedding. The probability of remaining at risk (ϕ) is, therefore $1 - \lambda$:

$$\phi = 1 - \lambda = \exp(-\exp(\gamma))$$

consistent with a discrete-time complementary log–log formulation. Re-encounter probability at time t (η_t) was modeled as a function of private recreational (Rec_t) and for-hire (FH_t) fishing effort:

$$\eta_{i,t} = \left(1 - \exp\left(-\exp\left(\alpha_0 + \alpha_1 \mathrm{Rec}_t + \alpha_2 \mathrm{FH}_t\right)\sigma_i\right)\right)$$

where α_0 is the baseline log-hazard of recapture (assumed to be close to 0 on the probability scale), while α_1 and α_2 denote the effects of private and for-hire recreational effort, respectively. The hazard of re-encounter for a given fish is scaled by size-selectivity σ_i based on the general circle hook selectivity curve presented in Garner et al. (2017) (Supplementary Figure S1).

In our framework, the parameters ψ_i (post-release survival) and ξ (reporting rate) appear only as the product $\breve{\psi} = \xi \times \psi_i$. As a consequence, they are structurally non-identifiable without external information. We therefore modeled *apparent* post-release survival:

$$\breve{\psi} = \xi \exp\left(\beta_0 + \sum_{k=1}^{K} \beta_k f_k(x_{i,k}|\theta_k)\right) = \exp\left(\breve{\beta}_0 + \sum_{k=1}^{K} \beta_k f_k(x_k|\theta_k)\right)$$

where $\breve{\beta}_0 = \log(\xi) + \beta_0$. Absolute survival of fish released under the best possible circumstances can be recovered by stipulating either β_0 or ξ from external data or as an assumption. This formulation follows the logic of relative risk models used in previous work (e.g., Hueter et al., 2006; Rudershausen et al., 2014; Sauls, 2014; Jackson et al., 2018; Runde et al., 2019).

Finally, because fish were tagged at spatially explicit locations that vary with regard to the intensity of private and for-hire recreational fishing effort, we modeled all components spatiotemporally. To balance spatial resolution with the need for sufficient sample sizes to enable reliable estimation, we binned fish into 0.25° × 0.25° latitude–longitude cells (≈ 668 km^2 each), yielding L = 16 spatially distinct cells (denoted locations $l \in \{1, 2, ...L\}$) for analyses (Figure 2). Proxies for private recreational effort at each time step t and spatial location l were derived from the Florida Fish and Wildlife (FWC) State Reef Fish Survey (SRFS) and for-hire effort was approximated using the Observer Program data. To facilitate model convergence, effort from each of the two fishing fleets was divided by the maximum observed value to generate scaled estimates ranging from 0 to 1.

It is important to note that both metrics are imperfect proxies for true spatiotemporal variation in recreational effort. Although uncertainty in these quantities is absorbed by α_0 (representing the log hazard of re-encounter in the absence of observed recreational effort), more precise and spatiotemporally resolved estimates of recreational effort could improve this methodology.

Under a general structure for post-release survival, the recapture probability for fish i at time t is:

$$Pr(R_i = t) = \breve{\psi}_i \prod_{s=t_{0[i]}}^{t-1} \left(\phi(1-\eta_{i,s,l[i]})\right) \phi\eta_{i,t,l[i]}$$

$$Pr(R_i = 0) = 1 - \sum_{t=t_{0[i]}}^{T} \left[\breve{\psi}_i \prod_{s=t_{0[i]}}^{t-1} \left(\phi(1-\eta_{i,s,l[i]})\right) \phi\eta_{i,t,l[i]}\right]$$

$$\phi = \exp\left(-\left(\exp(\gamma)\right)\right)$$

$$\eta_{i,t,l[i]} = \left(1 - \exp\left(-\exp\left(\alpha_0 + \alpha_1 \mathrm{Rec}_{t,l[i]} + \alpha_2 \mathrm{FH}_{t,l[i]}\right)\sigma_i\right)\right)$$

$$\breve{\psi}_i = \exp\left(\breve{\beta}_0 + \sum_{k=1}^{K} \beta_k f_k\left(x_{i,k} | \theta_k\right)\right)$$

$$\beta = -\exp(\rho)$$

$$\breve{\beta}_0 = -\exp(\breve{\rho}_0)$$

$$\breve{\rho}_0, \rho, \alpha_1, \alpha_2 \sim N(0,1)$$

$$\alpha_0 \sim N(-4, 1)$$

$$\gamma \sim N(-2.67, 1)$$

Here, the subscript $l[i]$ denotes the location l corresponding to fish i. The parameters $\breve{\rho}_0$, ρ, α_1, and α_2 were assigned naive, normally distributed priors with a mean of 0 and a standard deviation of 1, reflecting a reasonable degree of uncertainty in link-space. Meanwhile, the baseline probability of re-encounter α_0 was assigned a prior distribution of $N(-4,1)$ to reflect an *a priori* re-encounter probability of nearly 0 in the absence of recreational effort from either fleet. Similarly, we assigned a weakly informative $N(-2.67,1)$ prior to the log-hazard rate of loss, γ, derived from the annual natural mortality rate presented in SEDAR43 (2015). This value, 0.27, was scaled to a quarterly time step and converted to the log-hazard scale (i.e., $\log(-\log(1-\frac{0.27}{4})) \approx -2.67$). Priors for θ_k values are parameter and model-specific and detailed below in the Model specification section.

Notably, fish could be released at any time within the first interval, and thus may experience only a fraction of the interval survival and recapture probabilities. To account for this, we defined v_i as the fraction of the first interval experienced by fish i, based on its release date, and scaled ϕ_{t_0} and η_{i,t_0} accordingly:

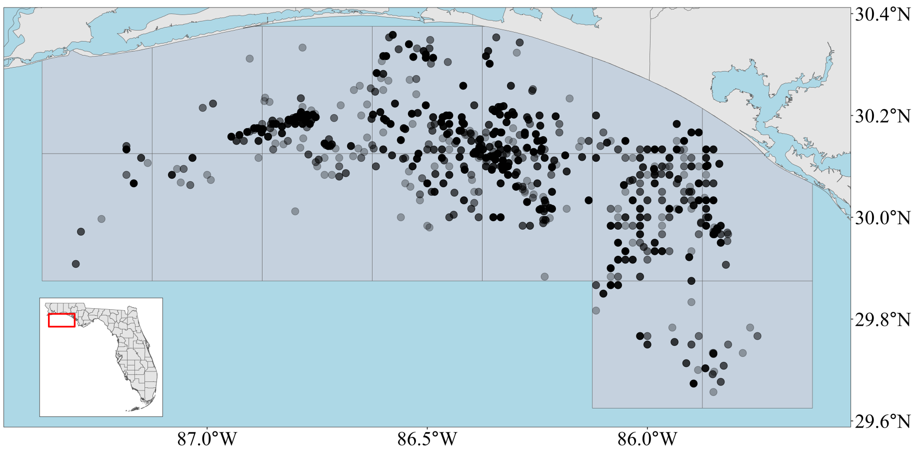

FIGURE 2
Map of tagged gray triggerfish release locations from 2022 through 2024 in the Florida Panhandle. Darker colors correspond to higher concentration of releases. Discrete spatial cells used for analysis are superimposed.

$$\phi_t^{(i)} = \begin{cases} \phi_t, & t > t_{0[i]} \\ \phi_t^{v_i}, & t = t_{0[i]} \end{cases}$$

$$\eta_{i,t,l[i]}^{(i)} = \begin{cases} \eta_{i,t,l[i]}, & t > t_{0[i]} \\ 1 - (1 - \eta_{i,t,l[i]})^{v_i}, & t = t_{0[i]} \end{cases}$$

This ensured that survival and recapture probabilities for partially experienced intervals are appropriately scaled for each fish.

2.2.1 Model specification

We evaluated several model structures (g_m) to relate capture-time predictors to apparent post-release survival ($\breve{\psi}$). Depth and SST were the primary variables of interest, given prior evidence of their influence on survival of released fish (Giomi et al., 2008; Gale et al., 2013; Runde et al., 2019; Bohaboy et al., 2020; Hyman et al., 2026). Because both factors are associated with physiological thresholds, we anticipated nonlinear effects. At shallow depths, barotrauma is negligible and survival is generally high; for example, studies of red grouper reported minimal effects in depths of less than 20 m (Burns, 2009). Beyond this threshold (i.e., depths greater than 20 m), swim bladders expand and may burst due to pressure changes, increasing the severity of barotrauma and elevating mortality risk. Similarly, moderate temperature increases may be tolerated, but survival is expected to decline once species-specific thermal tolerances are exceeded.

Our baseline model, g_0, did not include any predictors of survival and served as a null hypothesis for model comparison.

$$\breve{\psi}_i = \exp(\breve{\beta}_0)$$

The next model, g_1, posited a nonlinear effect of capture depth:

$$\breve{\psi}_i = \exp\left(\breve{\beta}_0 + \beta_D f(\text{Depth}_i|\theta_D)\right)$$

Where Depth_i is the fishing station depth at which fish i was initially caught and tagged, and the nonlinear transformation $f(\text{Depth}_i|\theta_D)$ is a modified softplus function defined as:

$$f(x|\theta_x) = \ln(1 + \exp(x - \theta_x)) - \ln(1 + \exp(-\theta_x))$$

Here, θ_D is the depth threshold where survival begins to decline, and β_D scales the steepness of the decline. Subtracting $\ln(1 + \exp(-\theta_x))$ centers the function such that $f(0) = 0$, improving interpretability and parameter identifiability. This transformation provided a smooth, threshold-like response, with shallow depths having little effect and deeper captures progressively reducing survival (Supplementary Figure S2). Meanwhile, θ_D was assigned a normal prior centered on 20 m with a standard deviation of 2.5, reflecting a plausible *a priori* range of threshold values between 10 m and 30 m.

Model g_2 extended this framework to include SST:

$$\breve{\psi}_i = \exp\left(\breve{\beta}_0 + \beta_D f(\text{Depth}_i|\,\theta_D) + \beta_T f(\text{SST}_i|\theta_T)\right)$$

where SST_i is the temperature at which fish i was initially caught and tagged, obtained via HYCOM; θ_T is the SST threshold, and β_T controls the rate of decline beyond this point. Reflecting the expectation that thermal stress would only manifest in warmer conditions, θ_T was assigned a normally distributed prior centered on 25°C with a standard deviation of 2.5. All three model formulations are summarized in Table 1.

2.2.2 Model implementation

We used the Stan probabilistic programming language (Gelman et al., 2015; Stan Development Team, 2023) within R to perform Bayesian inference. Each model was run with four parallel Markov chains using the "No U-Turn Sampler" (NUTS). Each chain consisted of 1,000 warm-up iterations followed by 1,000 sampling iterations, producing a total of 4,000 posterior draws. Convergence was determined using the $\hat{R}$ statistic (at convergence, $\hat{R} \approx 1$; Gelman et al., 2015). Covariates were considered scientifically meaningful if their 80% credible intervals (CIs) excluded zero. Unless otherwise noted, all reported estimates correspond to the maximum *a posteriori* (MAP) values and 80% CIs.

2.2.3 Model performance and selection

We evaluated model performance using the estimated log pointwise predictive density (ELPD) and corresponding Δ_{ELPD} values, which quantify the difference in predictive accuracy between each model and the best-performing model in the set (Vehtari et al., 2017). ELPD reflects out-of-sample predictive accuracy and was estimated via the approximate Leave-One-Out Information Criterion (LOO-IC) (Gelman et al., 2015; Vehtari et al., 2017), using the loo package (Vehtari et al., 2022). When models exhibited similar Δ_{ELPD} values (i.e., ≤ 4; Sivula et al., 2020), we selected the simpler model as the most parsimonious. The best-performing model, as determined by LOO-IC, was compared to a version with substantially weaker priors (variance set to 100) for threshold effects. Posterior distributions did not appreciably change, and we therefore concluded that the model was robust to modest variation in the choice of priors.

2.2.4 Counterfactual projections

To evaluate how predictors influenced gray triggerfish post-release survival, we developed conditional projections of mortality across counterfactual depth (20–70 m, in 1 m increments) and SST (15, 22.5, and 30°C) combinations, which correspond roughly to the range (depth) and minimum, median, and maximum (SST) values observed (i.e., $J = 50 \times 3 = 150$ combinations). Counterfactual predictors are denoted x^*. Because our relative risk framework does not directly yield absolute estimates of post-release survival,

TABLE 1 Candidate structures considered for relating depth and sea surface temperature (SST) to relative post-release survival.

Model	Formulation
g_0	$\breve{\psi}_i = \exp(\breve{\beta}_0)$
g_1	$\breve{\psi}_i = \exp(\breve{\beta}_0 + \beta_D f(\text{Depth}_i|\theta_D))$
g_2	$\breve{\psi}_i = \exp(\breve{\beta}_0 + \beta_D f(\text{Depth}_i|\,\theta_D) + \beta_T f(\text{SST}_i|\theta_T))$

projections required a baseline assumption. Here, $\tilde{\beta}_0$ denotes the log baseline survival expected when depth and SST exert negligible influence on post-release mortality. Following the approach of Sauls (2014), we report annual post-release mortality estimates assuming baseline survival probabilities of $\tilde{\beta}_0 \in \{0,-0.78,-0.16\}$, representing a plausible range of log values corresponding to baseline survival probabilities of 1, 0.925, and 0.85, respectively. For figures, we make the conservative assumption of a baseline survival probability of 1 (i.e., $\tilde{\beta}_0 = 0$).

Using posterior draws from the best-performing model, for each predictor combination j and posterior draw d, we computed the conditional post-release survival probability $\tilde{\psi}_j^{(d)}$ as:

$$\tilde{\psi}_j^{(d)} = \exp\left(\tilde{\beta}_0 + \sum_{k=1}^{K} \beta_k^{(d)} f_k(x_{j,k}^{\star} | \theta_k^{(d)})\right)$$

Post-release mortality was then calculated as $\tilde{\mu}_j^{(d)} = 1 - \tilde{\psi}_j^{(d)}$.

2.2.5 Posterior predictive estimates

Using Observer Program data as a proxy for the recreational fleet, we used the methodology defined in Section 2.2.4 to estimate expected post-release mortality for each month during 2022, 2023, and 2024, using recorded environmental variables. Using 1,000 posterior draws d, we estimated the average post-release mortality across all observations o as follows:

$$\tilde{\mu}_{\text{pred}}^{(d)} = \frac{1}{O} \sum_{o=1}^{I} \tilde{\mu}_o^{(d)}$$

The vector $\tilde{\mu}_{\text{pred}}$ for all 1,000 posterior draws represents the full posterior distribution of post-release mortality for the chosen temporal domain, given estimated coefficients and an assumed baseline post-release survival value. We applied this equation to estimate the posterior distribution of post-release mortality for: (1) each month across years and (2) each calendar year. Finally, to investigate how post-release mortality may have changed over time, we computed average annual estimates using the same methodology based on gray triggerfish caught and released as recorded by the Observer Program from 2015 to 2024 (i.e., hind-casts for the last 10 years). For hind-casts, the Observer Program data were limited to charter-mode trips, and post-release mortality was estimated accordingly under the assumption that the charter fleet provides a more accurate proxy for the broader private recreational fleet than head boats (Hyman et al., 2026). In all instances, applying for-hire charter data from the Observer Program to estimate recreational post-release mortality rates relies on the assumption that fishing practices are comparable between the charter and private recreational fleets. While this assumption is routinely made in stock assessments, given the limited information on discarding behavior in the private fleet, it has not been empirically tested.

2.2.6 Supporting information and code

To facilitate reproducibility, we have included all data and model code required to produce tables and figures in an online repository with companion R files with code annotations.

3 Results

In total, we analyzed tag-return data from 3,744 gray triggerfish caught and released along the Florida Panhandle from 2022 through 2024. Fishing station depth at the time of initial capture ranged from 20 to 67 m (median 33 m), whereas SST at the time of initial capture varied between 15 and 31°C (median 22°C). Preliminary data analysis suggested that the proportion of reported recaptures decreased with increasing depth and SST at capture (Figure 3), particularly at depths greater than 30 m and water temperatures greater than 20°C. The median time at large was 72 days (range: 1–832 days).

Model selection using LOO-IC suggested that model g_2 – which posited that post-release survival was proportional to a nonlinear function of depth and SST – yielded an optimal balance between predictive performance and model complexity. Its ELPD exceeded those of the null (g_0) and depth-only (g_1) models by 22.45 and 13.30 points, respectively, indicating superior predictive performance (Table 2). Posterior predictive checks showed strong agreement with the observed data (Supplementary Figures S3, S4). Thus, we selected model g_2 as the best model within the set.

Posterior distributions from model g_2 indicated that increases in local recreational effort from both fleets were associated with a higher probability of re-encounter. The intercept of the re-encounter component, α_0, was negative, suggesting that the probability of re-encountering a previously tagged gray triggerfish was low in the absence of observed recreational fishing activity (Table 3). The slope parameters relating re-encounter probability to both private and for-hire recreational fishing effort, α_1 and α_2, respectively, were positive, indicating that the probability of a gray triggerfish being recaptured, conditional on remaining at risk, increased with greater recreational effort. Finally, the posterior distribution of γ was negative, corresponding to an expected probability of remaining at risk within a three-month interval of 0.76 (80% CI: 0.69–0.84).

Posterior distributions and counterfactual projections suggested strong effects of depth and SST on post-release survival. The thresholds at which depth and SST began to impact post-release survival were 31.25 m (26.49–33.97 m) and 22.85°C (21.02–24.83°C), respectively, consistent with patterns observed in empirical data. Assuming a baseline post-release survival probability of 1 (i.e., 100% survival), the post-release mortality of fish captured in 15°C waters rose rapidly from approximately 0 at 20 m to 0.92 (0.83–0.97) at 70 m (Figure 4) due to the magnitude of the posterior distribution of β_D. At 30°C, the expected post-release mortality was 0.51 (0.41–0.59) at 20 m and 0.96 (0.91–0.98) at 70 m.

Using the full observer dataset from 2022 through 2024, posterior predictive estimates of monthly gray triggerfish post-release mortality, conditioned on baseline post-release survival of 1 (i.e., 100% survival), were lowest in February (MAP: 0.06; 80% CI: 0.03 – 0.13) and highest in August (0.65; 0.57 – 0.72; Figure 5A). Annual post-release mortality estimates remained relatively consistent across years, with MAP values of 0.34 (0.29 – 0.41) in 2022, 0.31 (0.25 – 0.40) in 2023, and 0.35 (0.29 – 0.42) in 2024 (Figure 5B). Conditioned on the lowest plausible baseline survival

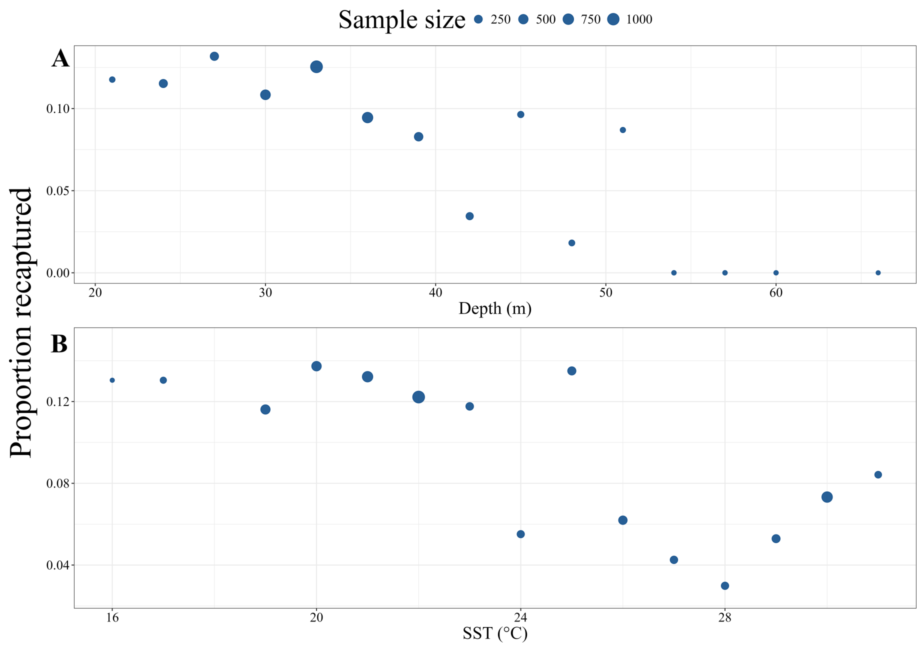

FIGURE 3
Proportions of gray triggerfish recaptured as a function of **(A)** depth (binned to 3 m intervals) and **(B)** sea surface temperature (SST: binned to 1°C intervals) based on raw data. Point size is relative to the number of tagged fish in each bin.

probability (0.85), seasonal patterns persisted, albeit at higher overall levels, and MAP estimates of annual post-release mortality were approximately 10% higher (0.44, 0.42, and 0.44 for 2022, 2023, and 2024, respectively; Table 4).

Long-term projections based on charter fishing station depth and SST from 2015 to 2024 indicated increasing post-release mortality of gray triggerfish over time. Relative to a baseline post-release survival of 1 (i.e., 100% survival), mortality was lowest in 2016 (MAP = 0.17; 80% CI: 0.13–0.24) and highest in 2020–2021 (0.43; 0.36–0.50; Figure 6).

4 Discussion

By leveraging a large-scale, long-term mark–recapture dataset, we provide dynamic estimates of gray triggerfish post-release mortality under realistic fishing conditions. Our modeling framework incorporated environmental drivers, such as fishing station depth and SST, while accounting for spatiotemporal variation in recreational fishing effort. This approach produced annual post-release mortality probabilities ranging from 0.25 to 0.51. These probabilities are consistent with findings presented by Runde et al. (2019) and Bohaboy et al. (2020), but are substantially higher than the values currently used in the most recent stock assessment (SEDAR43, 2015), which was conducted before this more recent body of work was available. Updating upcoming assessment inputs with empirically derived mortality estimates will improve the accuracy of stock status projections and yield.

Depth and SST both emerged as strong predictors of post-release mortality, with our flexible model revealing nonlinear

TABLE 2 Model selection results from three Bayesian discrete-time survival models (g_m) predicting gray triggerfish recapture.

Model	LOO	$ELPD_{LOO}$	$\Delta ELPD$	$SE\Delta_{ELPD}$
g_2	**3639.32**	**-1819.66**	**0.00**	**0.00**
g_1	3665.92	-1832.96	-13.30	5.62
g_0	3684.21	-1842.10	-22.45	7.09

Models are presented in order of predictive power based on the approximate Leave-One-Out Information Criterion (LOO). Associated values include $ELPD_{LOO}$: the estimated log-pointwise density calculated from LOO; Δ_{ELPD}: the relative difference between the ELPD of any model and the best model within the set; $SE_{\Delta ELPD}$: standard error for the pairwise differences in ELPD between the best model and any given model. The selected model (g_2) values are presented in bold font.

TABLE 3 Posterior summary statistics – maximum *a posteriori* (MAP) and 80% CI – of the predictor coefficients from our best-performing model (g_2).

Predictor	10%	MAP	90%
α_0	-1.22	-0.92	-0.65
α_1	0.28	1.23	2.12
α_1	0.47	0.83	1.17
γ	-1.75	-1.30	-0.99
β_D	-0.10	-0.06	-0.04
β_T	-0.16	-0.11	-0.08
β_T	26.49	31.25	33.97
θ_T	21.02	22.85	24.80

All values are rounded to two decimal places.

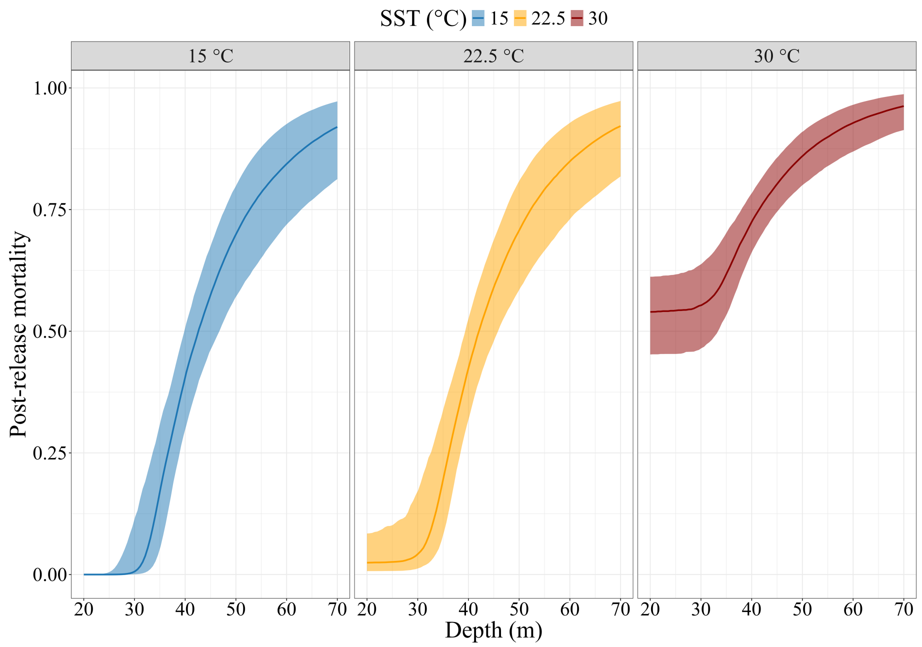

FIGURE 4
Conditional projections of the probability of post-release mortality as a function of depth and sea surface temperature (SST), assuming a baseline post-release survival value of 1 (i.e., 100% survival). Maximum *a posteriori* predictive expectations are denoted with lines, while 80% CIs are denoted with shaded bands.

relationships and thresholds that were not captured in earlier studies. Specifically, post-release mortality was relatively low at shallower depths and cooler temperatures but increased steeply beyond threshold ranges. The positive relationship between capture depth and mortality aligns with expectations based on barotrauma, which intensifies with increasing depth of capture (e.g., Ferter et al., 2015; Rankin et al., 2017; Runde et al., 2019; Bohaboy et al., 2020; Rudershausen et al., 2025; Ramsay et al., 2025). Gray triggerfish appear particularly vulnerable to barotrauma due to their laterally compressed morphology and rigid body wall, traits that may exacerbate internal organ trauma associated with swim bladder expansion. Consistent with this, Runde et al. (2019) reported significant organ damage in 69% of necropsies conducted on individuals captured between 30 and 45 m, including prolapsed intestines and livers and visceral intrusion into the gill arches. Notably, 75% of fish exhibiting substantial internal injuries showed no obvious external signs of barotrauma. This species-specific vulnerability underscores the importance of incorporating morphology and physiology into evaluations of post-release mortality, as reliance on generalized assumptions derived from more resilient taxa may substantially underestimate vulnerability for species with different body plans, such as gray triggerfish.

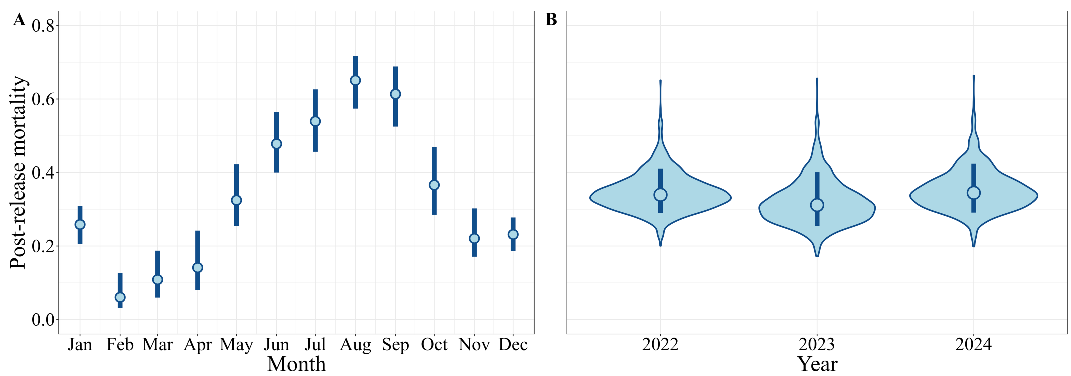

FIGURE 5
Monthly **(A)** and annual **(B)** posterior predictive distributions of gray triggerfish post-release mortality based on observer data from 2022 through 2024 conditioned on a baseline survival probability of 1 (i.e., 100% survival). In both panels, circles denote the *maximum a posteriori* predictive estimate, while bars denote the 80% CI. In panel B, a violin plot of the full posterior predictive distribution for each year is superimposed under the median value and 80% CI.

TABLE 4 Maximum *a posteriori* (MAP) values and 80% CI of predicted annual post-release mortality ($\tilde{\mu}_{pred}$) under varying baseline survival probability assumptions of 1 ($\tilde{\beta}_0$=0), 0.925 ($\tilde{\beta}_0$= -0.078), and 0.85 ($\tilde{\beta}_0$= - 0.16).

Year	$\tilde{\beta}_0$ = 0			$\tilde{\beta}_0$ = −0.078			$\tilde{\beta}_0$ = −0.16		
	10%	MAP	90%	10%	MAP	90%	10%	MAP	90%
2022	0.29	0.34	0.41	0.34	0.39	0.45	0.39	0.44	0.50
2023	0.25	0.31	0.40	0.31	0.36	0.44	0.36	0.42	0.49
2024	0.29	0.35	0.42	0.34	0.40	0.47	0.39	0.44	0.51

Sea surface temperature also elevated post-release mortality, consistent with a growing body of evidence that warmer waters amplify capture-related stressors (Olla et al., 1998; Gale et al., 2013; Curtis et al., 2015; Kraak et al., 2019). Elevated temperatures increase metabolic demand during the capture and recovery process (Rubalcaba et al., 2020), compounding physiological stress associated with handling and air exposure (Davis, 2002). Recent analyses further suggest that gray triggerfish may be particularly sensitive to thermal stress relative to other reef-associated fishes (Hyman et al., 2026), although the precise physiological mechanisms remain unresolved.

Importantly, this strong temperature dependence has direct implications for climate vulnerability. As ocean temperatures continue to rise, post-release mortality is likely to increase even in the absence of changes to fishing effort or practices, effectively reducing the resilience of the stock to recreational fishing pressure. In this context, post-release mortality becomes an environmentally mediated source of fishing mortality rather than a fixed parameter, challenging the assumption of stationarity implicit in many assessment and management frameworks.

The influence of SST detected here may also be partially confounded by seasonal variation in post-release predation risk. Bohaboy et al. (2020) documented high predation rates on released gray triggerfish, which may be exacerbated during warmer months when predator activity and metabolic demand are elevated (Curtis et al., 2015). Regardless of the precise mechanism, the consistent relationship between temperature and post-release mortality underscores the need for adaptive management strategies that explicitly account for temperature-driven changes in discard mortality. Such frameworks will be increasingly important as warming oceans shift both the magnitude and timing of discard-related mortality beyond historical norms.

The relationship between SST and post-release mortality observed here resulted in seasonal variation in post-release mortality in our projections, with the highest mortality occurring in summer months when SST was elevated and fishing tended to occur in deeper waters. These findings align with those reported by Hyman et al. (2026), which observed strong seasonality in gray triggerfish post-release condition, a proxy for mortality. Similar seasonal patterns have been reported for red snapper (*Lutjanus campechanus*), with elevated post-release mortality estimates consistently observed during summer months (Campbell et al., 2014; Curtis et al., 2015; Ramsay et al., 2025). Collectively, these findings underscore the importance of considering seasonality in post-release mortality estimates, particularly when fishing effort is unevenly distributed throughout the year.

Estimates across years revealed increasing post-release mortality rates over the past decade, coinciding with fishing in progressively deeper waters. Since 2015, the average fishing depth at which the charter fleet encounters and discards gray triggerfish has increased from 28 to 34 m (Hyman et al., 2026). Several non-mutually exclusive mechanisms may underlie this behavioral shift. Localized depletion or reduced catchability of nearshore stocks could incentivize anglers to fish deeper habitats to maintain catch rates, a pattern documented in other fisheries experiencing serial spatial depletion (Young et al., 2015; Beaudreau and Whitney, 2016). In parallel, continued advances in fishing technology—including improved sonar, GPS, and electric reels—have

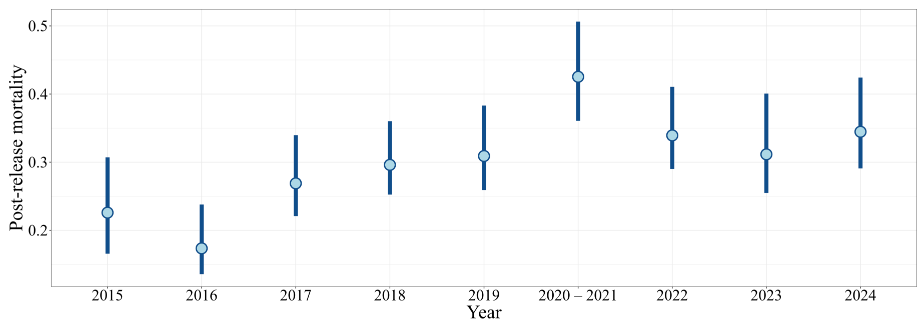

FIGURE 6
Posterior predictive distributions of gray triggerfish post-release mortality based on observer data from 2015 through 2024 conditioned on a baseline survival probability of 1 (i.e. 100% survival). Circles denote the maximum *a posteriori* predictive estimate, while bars denote the 80% CI. Data from 2020 and 2021 were pooled due to low sample size as a result of the COVID-19 pandemic.

substantially reduced the cost and risk of operating at greater depths, effectively expanding the accessible fishing footprint of the fleet (e.g., Beaudreau and Whitney, 2016). Regardless of the underlying cause, the observed temporal trend implies that post-release mortality is not only environmentally mediated but also behaviorally driven, reinforcing the need for assessment and management approaches that allow discard mortality to vary dynamically in response to changes in fleet behavior, technology, and stock distribution.

4.1 Implications for management

The immediate management implications of this work are two-fold. First, we estimated annual post-elease mortality, which was substantially higher than the values used in previous stock assessments (SEDAR43, 2015) and more consistent with the general range of 26 - 66% reported in recent literature (Runde et al., 2019; Bohaboy et al., 2020). Second, post-release mortality is not static; it varies both seasonally and inter-annually across environmental gradients such as depth and water temperature. Stock assessments that ignore this temporal and environmental variation risk biased estimates of dead discards and distorted evaluations of stock status. Incorporating dynamic, context-dependent mortality rates into the stock-assessment process will lead to better-informed and more effective management.

Our results suggest that post-release mortality is generally higher in deeper and warmer waters, which could inform targeted management strategies if stock status becomes impaired. For example, the current Gulf gray triggerfish recreational season includes months characterized by elevated SSTs and consequently higher associated discard mortality. Shifting open seasons to a cooler time of year could decrease discard rates in the absence of other co-occurring open fisheries (e.g., Hyman et al., 2025). However, implementing species-specific adaptive management strategies for reef fishes can be challenging, as multiple highly targeted species often co-occur spatially (Chagaris et al., 2019).

For instance, the recreational gray triggerfish fishery in Florida overlaps substantially with red snapper, perhaps the most prized recreational species in the Gulf (Gillig et al., 2000; Carter et al., 2015; Liese and Carter, 2017; Scyphers et al., 2021; Hyman et al., 2024). Consequently, gray triggerfish discard rates may remain elevated during summer months, when the red snapper fishery is open, regardless of species-specific temporal regulations for gray triggerfish. Managers must also balance the competing interests of an open-access, year-round recreational fishery with the effort-driven mortality associated with dead discards, making simultaneous closed seasons largely unfeasible. Higher discard mortality at deeper depths suggests that gray triggerfish may benefit from spatial management, such as limiting the fishery to shallower waters. However, many of the same challenges for seasonal closures outlined above are also present for spatial closures.

These interactions highlight the need for models of angler behavior, as well as explicit consideration of how regulatory changes influence effort redistribution, harvest, and dead discards across co-occurring species (Hyman et al., 2024, 2025). Nevertheless, adaptive strategies that account for spatial and temporal variability in post-release mortality may still reduce discard-related mortality while maintaining fishery access. As fluctuations and increases in ocean temperatures intensify and fishing practices continue to evolve, integrating temporally resolved, environmentally explicit mortality estimates into adaptive management frameworks will be critical for sustaining both short-term fishing opportunities and long-term population resilience.

4.2 Limitations and future work

A key simplifying assumption of our model is that fish re-encountered by anglers are permanently removed from the at-risk population, either through reporting (in which case the recapture is recorded and the fish is no longer tracked in our dataset), unreported harvest, or unreported re-release without a tag. This is improbable, as a fraction of re-encountered fish—particularly those not reported—are likely re-released with intact tags. This assumption was made due to the absence of reliable information on reporting rates, re-release probabilities, post–re-release mortality, and future environmental conditions at subsequent encounters.

The direction and magnitude of the bias introduced by this assumption depend on the relationship between mortality at initial release compared to subsequent re-releases. If post-release mortality probabilities are independent of one another (i.e., random with respect to the same covariates), then unobserved re-releases do not bias post-release mortality, as mortality terms cancel in expectation. In contrast, if post–release mortality probabilities follow similar processes across multiple re-releases, then mortality compounds multiplicatively with each additional encounter. Under this scenario, fish experiencing unfavorable post-release conditions (e.g., deep capture) are progressively less likely to remain in the population long enough to be recaptured and reported, leading to systematic underestimation of post-release mortality.

The true process likely lies between these extremes. Some post-release mortality determinants, such as SST at capture, vary temporally and may be weakly correlated across re-encounters, while others—most notably depth—are plausibly time-invariant due to relatively high site fidelity in gray triggerfish (Bohaboy et al., 2022). Consequently, depth-related effects on post-release mortality may compound across multiple re-releases, whereas temperature effects may partially average out. This raises the possibility that depth effects on post-release survival are conservatively estimated, although the magnitude of this bias cannot be resolved without explicit data on re-release behavior and survival.

We emphasize that this limitation is not unique to our study but applies broadly to relative risk models based on conventional tagging data, including logistic regression and Cox proportional hazards approaches, which similarly condition on first observed recapture and implicitly ignore unobserved re-releases. Addressing this issue will require either independent information on re-release and reporting probabilities or fully integrated state-space models that explicitly track repeated encounters.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material. Further inquiries can bedirected to the corresponding author. Observer Survey data is available upon request at atseaobserver@myfwc.com.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because gray triggerfish were tagged and released as part of standard recreational fishing activities conducted by permitted anglers. Tagging was nonlethal and followed protocols approved by the relevant management and regulatory entities. No fish were euthanized or held in captivity for the purposes of this study, and therefore formal animal ethics approval was not required under institutional guidelines.

Author contributions

AH: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. CR: Conceptualization, Methodology, Validation, Visualization, Writing – review & editing. SW: Conceptualization, Project administration, Supervision, Writing – review & editing. TF: Funding acquisition, Resources, Supervision, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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SUPPLEMENTARY FIGURE 1
Estimated general circle hook selectivity curve for gray triggerfish based on Garner et al. (2017). Selectivity for fish *i* is modeled as a as a function of fork length *l* using an exponential-logistic equation $\sigma_i = \frac{exp\ (\beta\alpha(\theta - l_i))}{1-\beta(1-exp\ (\alpha(\theta-l_i)))}$, where the estimates of α, β, and θ are 0.045, 0.254, and 332.8, respectively.

SUPPLEMENTARY FIGURE 2
Conceptual diagram demonstrating the effect of depth on relative post-release survival using a modified softplus function and log link with differing β_D values. The vertical line denotes the threshold θ_D after which increases in depth correspond with decreases in post-release survival. Here, log post-release baseline survival β_0 is set to 0.

SUPPLEMENTARY FIGURE 3
Posterior predictive checks for model g_2. **(A)** Distribution of simulated recapture proportions with the observed recapture proportion indicated by the vertical line. **(B)** Posterior predictive calibration plot showing agreement between predicted and observed recapture probabilities. Predicted probabilities were grouped into evenly spaced bins, with the mean posterior predicted probability (x-axis) compared against the observed proportion of recaptures (y-axis) in each bin. The dashed 1:1 line denotes perfect calibration; deviations reflect systematic bias in predicted recapture probabilities. **(C)** A comparison of the empirical distribution of observed recapture times to the distributions of 1,000 scans from the posterior predictive distribution. **(D)** Empirical cumulative distribution function (ECDF) of observed recapture times compared with ECDFs simulated from posterior predictive draws.

SUPPLEMENTARY FIGURE 4
Posterior predictive checks for model g_2 against **(A)** depth (m), **(B)** sea surface temperature (SST) (°C), and **(C)** size (fork length; mm). Dark points represent the observed proportion of fish recaptured within each depth, SST, or size bin (values rounded to the nearest whole unit), while light points show the median posterior-predicted proportion. Only bins with N $\geq$ 10 fish are shown to avoid spurious proportions arising from small sample sizes.

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